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Increased agonistic behavior in hummingbirds (Family Trochilidae) in Monteverde, Costa Rica with a reduction of food at artificial feeders

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ABSTRACT

This study looked at the change in agonistic behaviors of hummingbirds (Family Trochilidae) with the reduction of an established food source at la Estación Biológica de Monteverde (1567m elevation), Costa Rica. There were three treatment periods: three feeders (ten days), one feeder (six days; reduction of food source), and three feeders (four days) between October 23 and November 14, 2005. The agonistic behaviors were the number of agonistic behaviors were recorded a well as the species composition of aggressors versus recipients. Over the three treatment periods there was an increase in hummingbird visits (treatment one to treatment two: $p = 0.0030$; treatment one to treatment three: $p = 0.0005$), agonistic behavior when the food source was reduced ($p = 0.0148$), and tolerance when the food source was replenished ($p = 0.0412$). The four dominant aggressors were: *Lampornis calolaem,* purple throated mountain gem, *Eupherusa eximia,* striped tailed hummingbird, *Colibri thalassinus*, green violet ear and *Campylopterus hemileucurus*, violet sabrewing; the three most targeted recipients were: *E. eximia*, *C. thalassinus* and *C. hemileucurus*. The artificial feeders increased agonistic behavior such as guarding and darting. This increase potentially occurred because it was more advantageous for the birds to guard the feeders, a constant, rich food source, than to trapline. Such behavior may cause an increase in territoriality and an alteration of the pollination system in areas with established artificial feeder gardens.

RESUMEN

El propósito de esta investigación fue determinar el cambio en el comportamiento agresivo de los colibríes de la familia Trochilidae con la reducción de un recurso de alimentario en la Estación Biológica de Monteverde (a 1567m de altitud), Costa Rica. Hubo tres períodos de tratamientos: tres comederos (con diez días de duración), un comedero (con seis días de duración y con una reducción de alimento), y tres comederos (con una duración de cuatro días) del 23 de Octobre al 14 de Noviembre de 2005. Los comportamientos agresivos fueron anotados de acuerdo al número de incidentes y a cuáles pájaros fueron los agresores y cuáles fueron los recipientes. En los tres tratamientos aumentaron las visitas de los colibríes (Del tratamiento uno al dos: $p = 0.0030$; del tratamiento uno al tres: $p = 0.0005$), así como los comportamientos agresivos cuando la fuente de alimiento fue reducida ($p = 0.0148$) y la tolerancia cuando se reestableció el recurso ($p = 0.0412$). Los colibríes más dominantes fueron *Lampornis calolaem, Eupherusa eximia*, *Colibri thalassinus* y *Campylopterus hemileucurus*; los colibríes que recibieron más comportamientos agresivos fueron *E. eximia*, *C. thalassinus*, y *C. hemileucurus.* El aumento en los comportamientos agresivos fue causado por los comederos artificiales. Tal vez esto sucedió

porque fue más beneficioso para los påjaros proteger los comederos, un recurso constante, que trasladarse para alimentarse en otros lugares. Este comportamiento de protección pudo causar un aumento en la territorialidad y una alteración en los sistemas de polinización en las áreas con comederos artificiales.

INTRODUCTION

Hummingbird (Family Trochilidae) anatomy, behavior, and social interactions are of interest to many, whether they be researching scientists or tourists at an artificial hummingbird garden. All 330 species have similar diet, anatomical features, high wing beat rates, and the ability to hover (Stiles and Skutch 1989). Therefore, niche partitioning is extremely important. It has allowed for different species to coexist in relatively similar and close habitats, while reducing the need to fight over resources (Stiles and Skutch 1989).

Hummingbirds must spend much of their time feeding in order to maintain their body temperature, despite efficient (95%) sugar assimilation (McWhorter and Martinez del Rio 2000). It is thought that hummingbird body size and feeding morphologies have closely coevolved (Altshuler and Dudley 2002; Suarez and Gass 2002). They lose a lot of energy due to their small size and rapid wing beat rate of up to 80 beats/second. Therefore, in order to sustain their high metabolic rate, the highest time-averaged metabolic rate among vertebrates (Voigt and Winter 1999; Suarez and Gass 2002), they must change their feeding behavior and social interactions to most efficiently access food (Altshuler 2004).

Stiles and Skutch (1989) state that most hummingbirds are aggressive towards others, regardless of species or sex, at flowers or feeding sites. Social status of the species greatly affects access to nectar sources and quality (Bleisweiss 1999); males are more dominant over conspecific females and species specific hierarchies are often set up at nectar sources (Bleisweiss 1999). These birds often hold feeding territories at consistent feeding locations. There are also trapliners, species that are typically less aggressive and visit many widely spread flowersinstead of maintaining a single permanent feeding territory. Traplining species are important pollinators because they carry pollen from one flower to another away from the source (Castellanos *et al.* 2003), and outcrossing confers fitness for plants.

Canela and Sazima (2003) noted that hummingbird feeding behavior could change depending on the food source. They found, in a study on the pollination of *Aechmea pectinata* (Bromeliaceae) in submontane rainforest in southeastern Brazil, that clumped flowering prompted territorial behavior in hummingbirds. Weidner (2001) found that *Amazilia tzactl*, the rufous-tailed hummingbird, was extremely aggressive and dominat, thereby reducing the number of other species at feeding sites. Other species, such as *Campylopterus hemileucurus*, the violet sabrewing, are known to be trapliners and are nonterritorial much of the time (Stiles and Skutch 1989). However, at sites using artificial feeders as the food source *C. hemileucurus* can be very agonistic (Weidner 2001).

This study examined the changes in hummingbird behavior and aggression in response to a reduction in food source. It specifically looked at which species of hummingbirds visited the feeders, their agonistic behaviors, and how their behavior changed with a reduction in food source. It was hypothesized that as the number of feeders decreased, agonistic behavior between species would increase, and upon food source replenishment tolerance between species would increase. This study showed species-species reactions to clumped food sources and identifies species which are more likely to succeed in food acquisition in areas with reduced food sources;

thereby, increasing the understanding of the effects of artificial feeding gardens on hummingbird behavior.

METHODS

The data were taken between October 23, 2005 and November 14, 2005 at la Estación Biológica de Monteverde, Costa Rica (1567 m elevation) (Fig. 1a). The study site was located adjacent to lower montane wet forest. There were two sites with red feeders (red attracts hummingbirds) placed in the same small field, which acted as replicates of one another; one was placed three meters from the intact forest edge and the other was placed twenty meters from the same forest edge, next to a large patch of bushes (Fig. 1b). The feeders were hung two meters off the ground using a blue nylon rope suspended between two trees, and were filled every morning with one liter of 30% sucrose solution each. The feeding sites were set up three days prior to the first treatment. There were three treatment periods: the first test period had three feeders (ten day duration), the second treatment period had one feeder (six day duration), and the third treatment period had three feeders (four days duration).

Hummingbird interactions were recorded in one-hour increments at 9:00AM, 10:00AM, 11:00AM, and 12:00PM and the observation period began ten minutes after arrival, to allow hummingbirds to acclimate to the presence of the observer. The number of visits per species was recorded, as were the following agonistic behaviors: *Darting, Calling, Striking, Plumage, Ignore* and *Guarding*. A *Visit* was defined as: arrival at the feeder, feeding (any number of times), and leaving the feeder. No agonistic behaviors were considered unless associated with a visit or arrival at a feeder. The agonistic behaviors were qualified as: *Darting*- flying at or chasing another resident or incoming individual, *Calling*- warning calls described by Stiles and Skutch (1989), *Plumage*- ruffling of head and neck feathers in display to another resident or visitor, *Ignore*- a resident individual allowing a visitor to feed, and *Guarding*- perching near the feeder site and confronting visitors. A total of 53 hours of observations were conducted. Treatment period versus total visitations, individual and total agonistic behaviors, were analyzed using Fisher's statistical test.

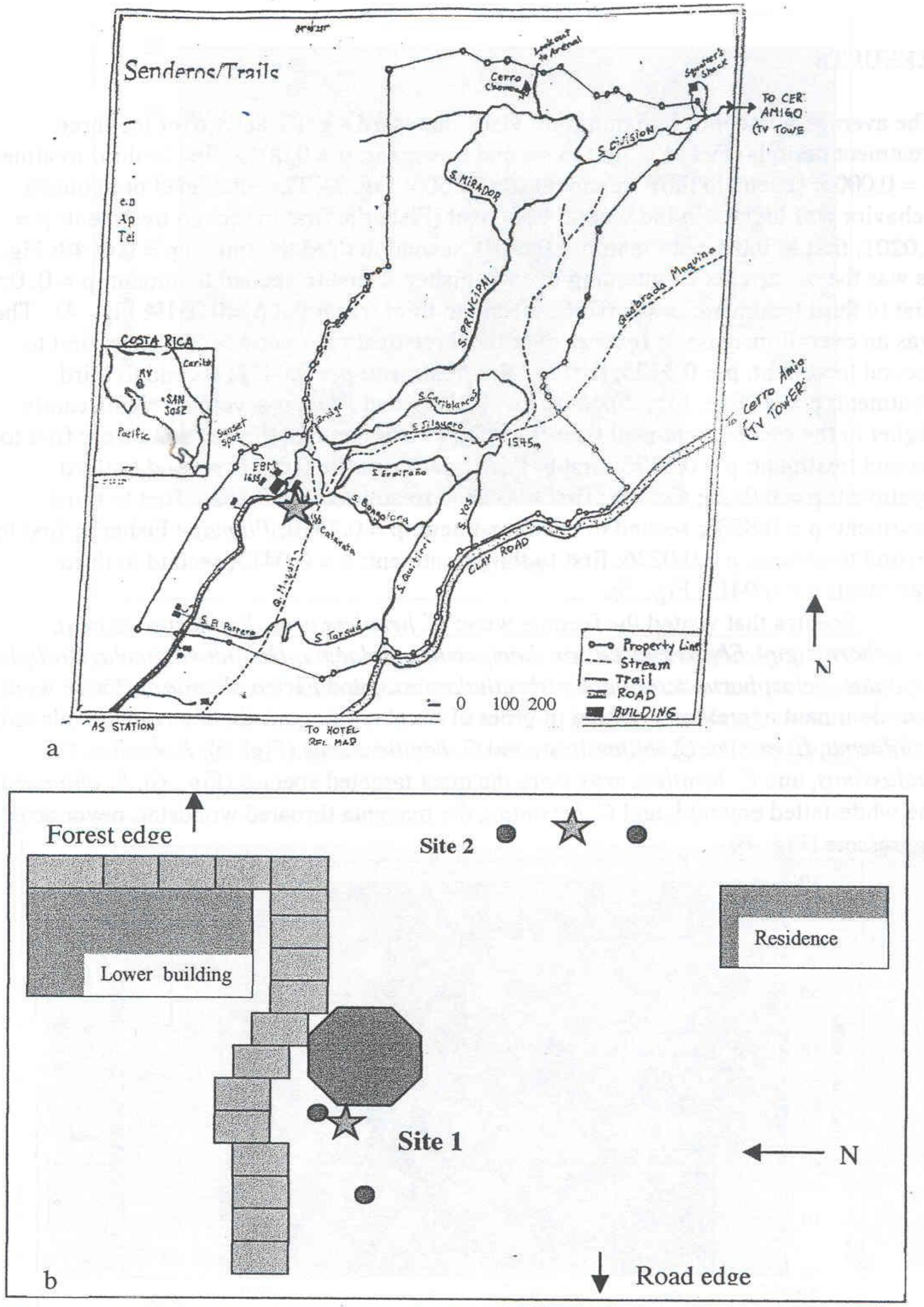


Figure 1. Study site at la Estación Biológica de Monteverde (1567 m elevation), Costa Rica. (a) The blue star marks the place where the two red feeder sites were set up. (b) The blue stars indicate the study sites, brown circles were utilized trees, the green octagon represents mixed vegetation on the site, and the grey square was the walkway. Observations made over the testing period of October 23 to November 14, 2005.

RESULTS

The average number of hummingbird visits increased significantly over the three treatment periods (Fisher's: first to second treatment: p = 0.0030; first to third treatment: p = 0.0005; second to third treatment p = 0.8606; Fig. 2). The total level of agonistic behavior was highest in the second treatment (Fisher's: first to second treatment: p = 0.0201; first to third treatment: p = 0.6439; second to third treatment: p = 0.0148; Fig. 3), as was the occurrence of guarding events (Fisher's: first to second treatment: p = 0. 0524; first to third treatment: p = 0. 6796; second to third treatment p = 0.0319; Fig. 4). There was an overall increase in *Ignores* over the three treatment periods (Fisher's: first to second treatment: p = 0.3125; first to third treatment: p = 0.0412; second to third treatment: p = 0.2816; Fig. 5). *Darting*, *Calling* and *Plumage* were all significantly higher in the second treatment than the other two treatments (Fisher's *Darting:* first to second treatment: p = 0.0176; first to third treatment: p = 0.0125; second to third treatment: p = 0.0125; *Calling:* first to second treatment: p = 0.1624; first to third treatment: p = 0.8588; second to third treatment: p = 0.2810; *Plumage* Fisher's: first to second treatment: p = 0.0236; first to third treatment: p = 0.0413; second to third treatment: p = 0.0413; Fig. 5).

Species that visited the feeders were: *C. hemileucurus, Eupherusa eximia, Phaethornis guy, Elvira cupreiceps, Lampornis calolaema, Heliodoxa jacula, Calliphlox bryantae, Selasphorus scintilla, Colibri thalassinus,* and *Elvira chionura*. There were four dominant aggressors, written in order of number of agonistic behaviors displayed: *L. calolaema*, *E. eximia*, *C. thalassinus*, and *C. hemileucurus* (Fig. 6). *E. eximia*, *C. thalassinus*, and *C. hemileucurus* were the most targeted species (Fig. 6). *E. chionura,* the white-tailed emerald, and *C. bryantae*, the magenta throated woodstar, never acted as aggressors (Fig. 6).

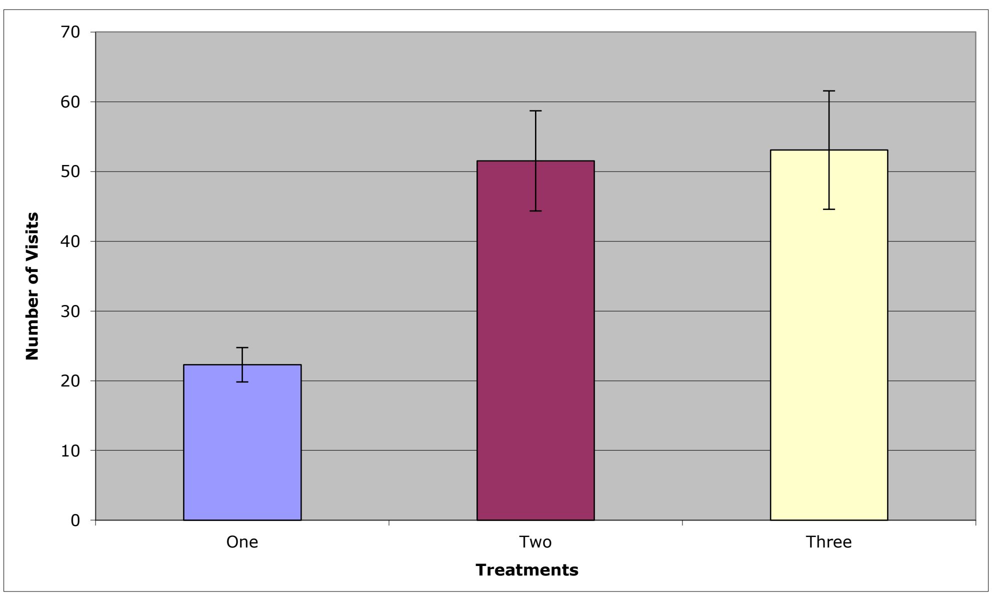


Figure 2. The mean number of hummingbird visits to artificial feeders, at la Estación Biológica de Monteverde in October and November, 2005, over three treatment periods: treatment one was three feeders (ten days), treatment two was one feeder (six days), and treatment three was three feeders (four days). n = 53.

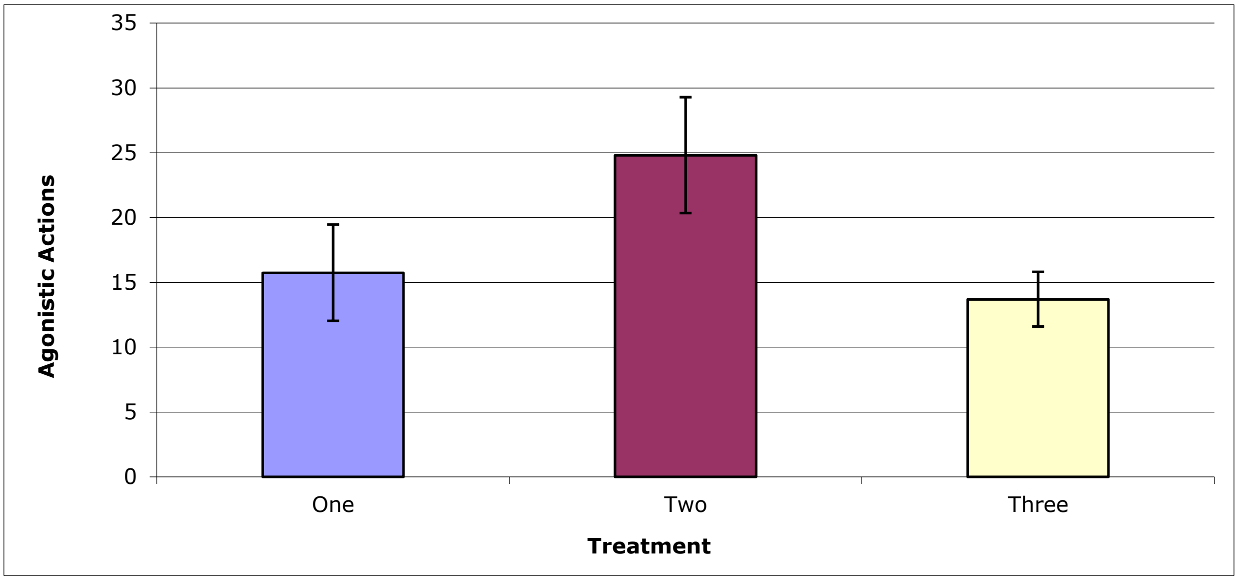


Figure 3. The mean number of agonistic events in hummingbirds, at artificial feeders, at la Estación Biológica de Monteverde in October and November, 2005, over three treatments treatment one was three feeders (ten days), treatment two was one feeder (six days), and treatment three was three feeders (four days). n = 53.

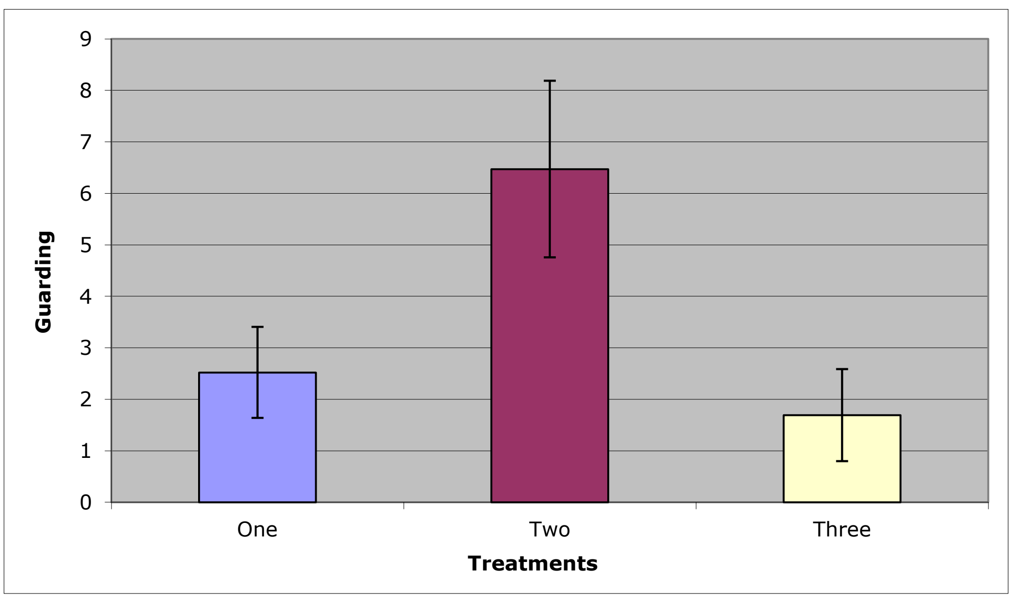


Figure 4. The mean number of guarding events in hummingbirds, at artificial feeders, at la Estación Biológica de Monteverde in October and November, 2005, over three treatments: treatment one was three feeders (ten days), treatment two was one feeder (six days), and treatment three was three feeders (four days). n = 53.

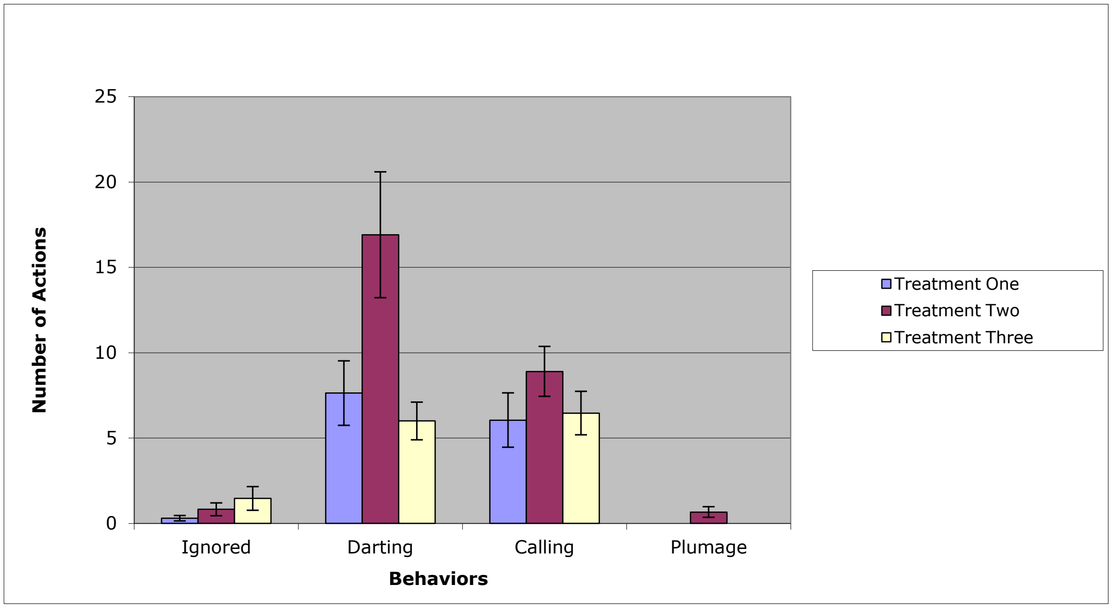
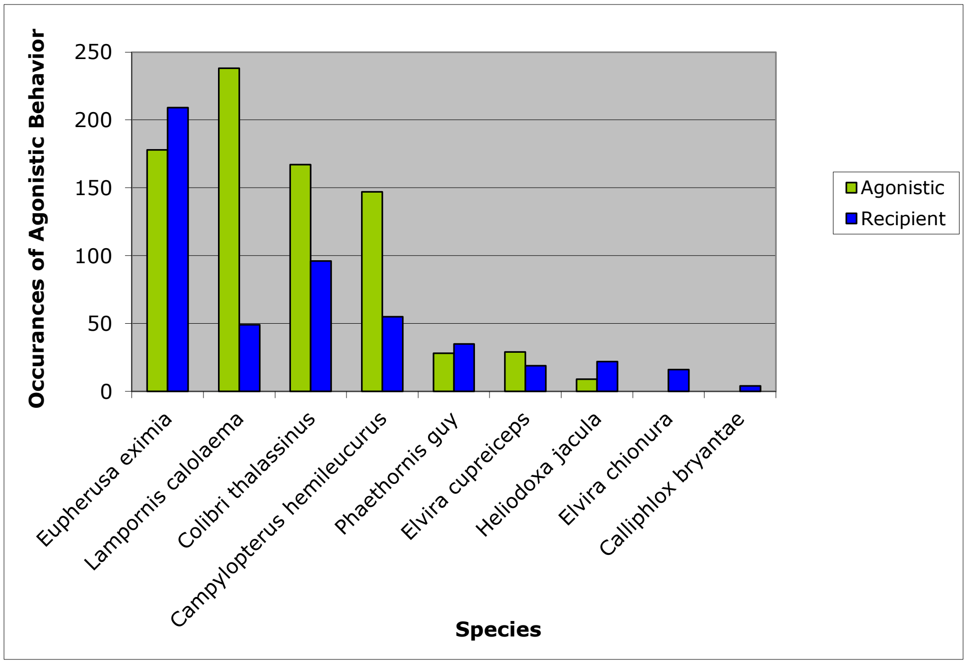


Figure 5. The mean number of agonistic behaviors (Ignored, Darting, Calling, and Plumage) in hummingbirds at artificial feeders at la Estación Biológica de Monteverde in October and November, 2005, over three treatment periods: treatment one was ten days (with three feeders), treatment two was six days (with one feeders) and treatment three was four days (with three feeders). n = 53.



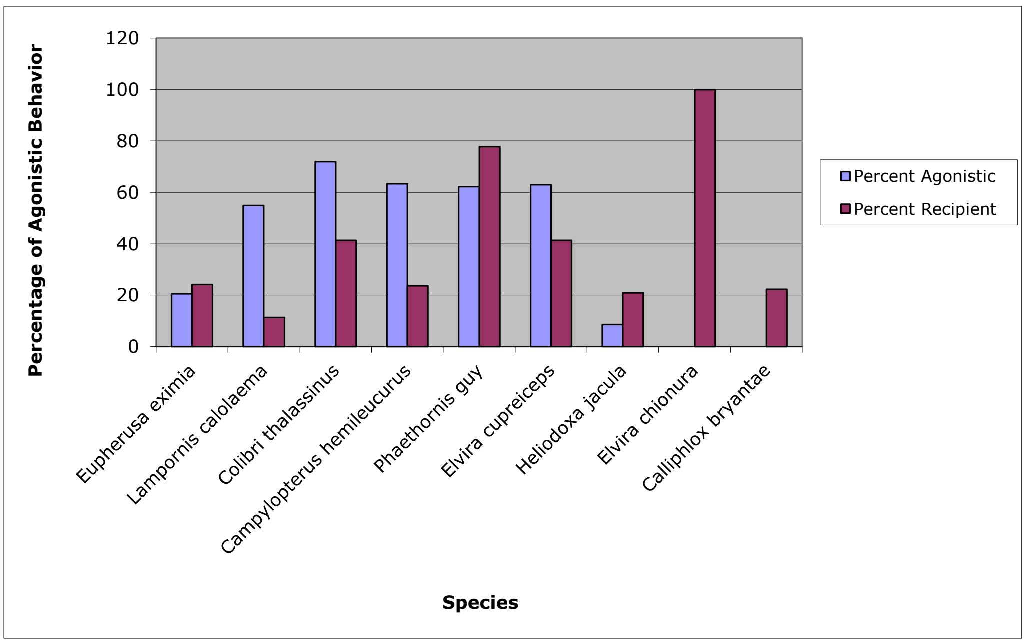


Figure 6. The number of aggressor and recipient events between hummingbirds at artificial feeders at la Estación Biológica de Monteverde. (a) Number of occurrence, (b) the percentage of agonistic behavior per species. October and November, 2005. n = 53.

DISCUSSION

This study showed that hummingbirds increase agonistic behaviors when a constant food source is suddenly limited. The first treatment acted as an acclimatizing period and created a consistent and reliable food source. It was more energetically advantageous for the birds to visit this one ample food source and protect it from others, than it would have been to feed as trapliners, even when the food source was limited. The increase in *Guarding* in the second treatment represented an increase in territoriality; this is most likely because sharing resources or tolerating other species causes a reduction in fitness when food is limited. The observed increase in tolerance (increase in *Ignores*) after the replenishing of the food source further supports the idea that as more food becomes available, birds are more likely to 'share' or tolerate others.

The average number of visitations increased over all three treatments. This is surprising because a decrease in visitations would be expected in the second treatment with resource reduction. Hypothetically less agonistic species would always be chased feeders in this scenario and would therefore stop wasting energy trying to utilize feeders. The observed increase could be due to gradual learning by hummingbirds that this was a consistent food source. Therefore, the increase in visitation is probably the result of more individuals having learned of the presence of the food source and consequentially more individuals feeding.

The increase in territoriality around artificial feeders has important implications for pollination. Castellanos et al. (2003) found that hummingbirds are actually better cross pollinators than other similar pollinators, such as bees. This is because they are larger and remove more pollen from a given flower. Additionally, removed pollen remains on their body longer, and more pollen is then transferred between flowers. Hence, aggregation leads to a decrease in pollen transfer, both in distance and occurrence, leading to greater selfing and reduced cross-pollination.

Aldrich and Hamrick (1998) found an important connection between territoriality and clumped resources. In fragmented forests, where food was more clumped, hummingbird territoriality significantly increased. They also found that on trees with larger patches of flowers, such as in pastures, higher territoriality resulted in an increased rate of selfing (Aldrich and Hamrick 1998). Therefore, as flower patches are reduced, there will be an even larger incidence of territoriality and reduction in traplining. This study showed that an increase in territoriality occurred in some species with the reduction of food. It should not be generalized to all hummingbird species, but territorial hummingbirds will probably respond by narrowing their feeding ranges, which would reduce cross-pollination. *C. hemileucurus*, which displays both territorial and traplining behavior, showed high levels of territoriality at the artificial feeders, therefore reducing their traplining behaviors. The behavioral change may be most drastic in these species, which vary between territoriality and traplining.

Suarez and Gass (2002) found that birds showed a preference for higher sucrose food sources, and many the sucrose solutions found in artificial feeders have higher sucrose concentrations than nectar found in flowers. This, coupled with the constancy of artificial feeders, implies that when given the choice between flowers and artificial feeders hummingbirds will choose the artificial feeding gardens. McWhorter and Martinez del Rio (2000) also found that hummingbirds showed a decrease in number of visits when sucrose concentrations were increased. Therefore, high sucrose concentrations found in artificial feeders cause both higher territoriality and lower feeding rates, as compared to visiting flowers, therefore reducing frequency of feeding. Presumably, this causes a decrease in pollination in general, specifically cross-pollination.

The four most dominant aggressors, *L. calolaema*, *E. eximia*, *C. thalassinus*, and *C. hemileucurus*, were assumed to show a higher advantage in situations with fewer feeding sites because they were the dominant species when vying for the limited food source. Interestingly three of these species, *E. eximia*, *C. thalassinus*, and *C. hemileucurus*, were most targeted recipients because they are all extremely territorial and spend much of their time near the feeders. This meant that these species were interspecifically fighting amongst eachother. It should also be noted that when looking at the percentages, rather than number of interactions, *E. chionura* and *P. guy* were most commonly targeted. These two species, according to Stiles and Skutch (1989), are typically trapliners and therefore, they probably only stopped at the feeders when passing between flowers. In these instances they were targeted by the more agonistic species.

E. chionura and *C. bryantae* never acted as aggressors. This was expected for *E. chionura* because they are very passive, but it was unexpected for *C. bryantae*. Stiles and Skutch (1989) described this species as a very agonistic and territorial species. Therefore, the lack of agonistic behavior was probably due to the low number of visits to the feeder.

It was also noted that there were very few females visiting the feeders, only two species, *E. eximia* and *L. calolaema,* had female visitors. This is probably due to the sexual dimorphism seen between males and females; females are often found at poorer food sources (Bleisweiss 1999) because males tend to be more dominant and territorial. This is also evidence that these artificial feeders were considered a good feeding source by the hummingbirds.

It was noted that hummingbirds, within one hour of the original feeder set up, had abandoned natural feeding habitats and were instead feeding solely at artificial feeders. This problem is compounded with the increase in artificial feeding gardens in areas for tourism, which induces territoriality by clumping a constant, high sucrose food source. Therefore, in areas with the artificial feeding gardens, pollination systems are likely to be disrupted. This is because the more agonistic species, *L. calolaema*, *E. eximia*, *C. thalassinus* and *C. hemileucurus,* which were described by Stiles and Skutch (1989) as either territorial and agonistic or potentially territorial, were also the most common visitors. Species described as trapliners (Stiles and Skutch 1989), for example *P. guy* and *E. chionura*, did not begin to congregate around the feeders as did the agonistic species. Therefore, the biggest impact on social dynamic and behavior in hummingbirds was on the territorial and more agonistic species, and less, at least to begin with, on the trapliners.

These artificial feeders also change the social dynamic within the species because they eliminate the naturally imposed effects of niche differentiation, because all the birds can feed at the nonspecialized feeders. At these artificial gardens there are interspecific interactions which would not normally have occurred in natural settings, partly because many of these species do not naturally co-occur. This changes the system imposed by natural resource availability, which is reduced or eliminated at these artificial feeders.

Future research should be done to see how the pollination rates for plants, commonly pollinated by more territorial species, change with distance from artificial feeders. If feeders induce increased territoriality in agonistic species, then they will be even less likely to trapline. Three examples of plant species pollinated by several of the above agonistic species were: *Heliconia* sp. (pollinated by *C. hemileucurus), Inga* sp. (pollinated by *E. eximia* and *C. bryantae*-described as agonistic), and *Cephaelis* sp. (pollinated by *C. hemileucurus* and *L. calolaema)* (Stiles and Skutch 1989). It would also be important to investigate the long-term effects on social dynamics at feeder gardens, to see how they are changing the behavior of trapliners and the less dominant species. Another helpful study would be to study the change in behavioral interactions between species, that do not naturally co-occur, at artificial feeding gardens.

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